EFFECTS OF RISING SEA SURFACE TEMPERATURE AND DECREASING SALINITY ON KELPS AND ASSOCIATED MACROALGAL COMMUNITIES

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A

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Abstract

Kelp forests provide a multitude of vital ecosystems services, such as habitat for commercially and recreationally important species, support of complex food webs, and reduction of coastal erosion. The diversity and resilience of kelp forest communities are threatened as the severity of climate change and other anthropogenic stressors continues to mount. Particularly in the North Pacific, sea surface temperature (SST) is warming and glacier melt is discharging into coastal waters, causing decreases in salinity. This study assesses possible impacts of increasing SST and decreasing salinity on kelp forests by examining the response of key kelp species and their associated macroalgal community to these parameters in a North Pacific estuary, using Kachemak Bay as a model system. This two-part study combines both 1) a retrospective analysis of effects of environmental variables on existing kelp populations (*Agarum clathratum*, *Laminaria yezoensis*, and *Saccharina latissima*) and their associated macroalgal communities at three discreet water depths (5, 10 and 15 m), and 2) a factorial laboratory experiment investigating the effects of rising SST and decreasing salinity on kelp spore settlement and initial gametophyte growth in *Eualaria fistulosa*, *Nereocystis luetkeana*, and *S. latissima*. No strong correlations were observed between adult kelp biomass of any individual species with past SST and salinity changes, with the exception of a negative correlation between SST and *L. yezoensis* biomass at 10 m. In addition, SST and salinity were insignificant factors in shaping the associated macroalgal community biomass. In contrast to the retrospective analyses, the experimental results indicated that the early life-history stages of all kelp study species experienced decreased settlement and growth at elevated temperatures and decreased salinities. *Eualaria fistulosa* spores and gametophytes were the most negatively impacted, compared to the more widely distributed *N. luetkeana* and *S. latissima*. These results suggest that *N. luetkeana* and *S. latissima* are more likely to outperform *E. fistulosa* under projected conditions. By exploring how both early and late life-history stages of several key kelp species are impacted by dual stressors, this research enhances our understanding of how these species and their associated macroalgal communities will respond to projected changes in SST and salinity.

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INTRODUCTION:

Kelp forests, common features along most temperate coastlines, provide numerous vital ecosystem services. Kelps are foundation species, providing essential nursery and adult habitat for commercially, recreationally and ecologically important fish and invertebrate species (Dayton 1985, Bologna & Steneck 1993, Seitz et al. 2014, Thornton & Herbert 2014). They support a wide range of trophic levels via complex food webs (Schiel & Foster 2006, Lorensten et al. 2010). Kelp forests also reduce coastal erosion via wave dampening (Neal et al. 2010). Furthermore, they are significantly more productive than many other marine habitats (e.g., open ocean, nearshore sandy habitats) (Duggins et al. 1989). For instance, *Macrocystis pyrifera* kelp forests in California boast an average ecosystem net primary productivity (NPP) of 2.8 ± 0.6 g C m^{-2} d^{-1} (Miller et al. 2011). Additionally, kelp forests play a key role in offshore nutrient cycling and act as a dispersal mechanism for many fish and invertebrate species, with drift kelp providing a vector for larval transport (Hinojosa et al. 2011). Largely because of their important ecosystem functions, it is critical that we assess the impacts of climate change on kelp forests while there is still time for mitigation.

Continued increases in sea surface temperature (SST) negatively impact many marine ecosystems (Hoegh-Guldberg & Bruno 2010). For example, seawater warming trends can result in range shifts of warmer-water species that outcompete resident species, already metabolically stressed under rising temperatures (Ling et al. 2009, Hoegh-Guldberg & Bruno 2010). From 1960 to 1990, SST increased by 0.14° ± 0.04°C per decade on a global scale (Casey & Cornillon 2001). However, it is suspected that this global warming trend is severely underestimated in many nearshore marine systems where increases in SST are projected to be ten times greater, as direct anthropogenic warming of the coastal zone results from nearby urban developments (Amos et al. 2013). On the Gulf of Alaska shelf in particular, records from the last 45 years indicate that the upper 100 m is warming at a rate of ~0.20°C $decade^{-1}$ (Royer & Grosch 2006, Kelly 2015). If this upward trend continues, an increase of ~2.0°C would be expected in this region in the next century. Additionally, climate change is likely to result in increased glacial melt, which will decrease the salinity of estuarine waters (Dyurgerov & Meier 2005). Modest projections indicate that the North Pacific is expected to see an overall 0.005/decade decrease in salinity (Boyer et al. 2005). On the Gulf of Alaska shelf, salinities in

the upper 100 m have decreased by ~0.15 decade^{-1} since 1970 (Kelly 2015). If this downward trend continues, a ~1.5 decrease in salinity would be expected in this region in the next century. High-latitude coastal regions are likely to experience accelerated decreases in salinity, given their proximity to melting glaciers and projected increases in precipitation, in southern Alaska in particular (Arendt et al. 2009, Bieniek et al. 2014). Furthermore, the northern Gulf of Alaska is home to the largest freshwater discharge system in North America, with a 62% greater freshwater input than that of the Mississippi River (Royer 1982, Atkinson & Grosch 1999). Increased freshwater discharge in North Pacific coastal systems will not only drive salinity down, it will also result in increased sediment suspension that will affect photosynthetic capacity and possibly further intensify impacts of rising SST and decreasing salinity on kelp forest communities (Wiencke et al. 2007, Spurkland & Iken 2011).

Climate change induced stressors, like increasing SST and decreasing salinity, are likely to play key roles in shaping kelp forests in the near future. Rising seawater temperatures have been linked to kelp forests undergoing phase shifts, resulting in less biodiverse, less productive algal-turf-dominated systems or urchin barrens (Connell & Russell 2010, Krumhansl et al. 2014). Metabolic adjustments in some kelp species, while allowing them to persist in the face of warming waters, have resulted in an overall decrease in resilience due to reduced ecological performance by kelp recruits (Wernberg et al. 2010). This is likely because microscopic, young stages of kelp species are more susceptible to temperature and salinity fluctuations than their mature counterparts (Fredersdorf et al. 2009). The negative impacts of temperature and salinity on kelp (e.g., inhibition of photosynthetic activity and reduction of germination capacity) occur to a greater extent under the concurrent stress of both factors, as they are thought to interact synergistically (Fredersdorf et al. 2009). Furthermore, it is important to examine species-specific responses to these dual stressors, as the species of kelp that comprise a forest can greatly impact associated community composition. For example, sites with both canopy and understory kelp species offer greater structural complexity than those with understory species alone, and are capable of supporting higher densities of fish accordingly (Bodkin 1986, Hamilton & Konar 2007). Although generally negative impacts of rising SST and decreasing salinity on kelp forests are supported by some studies, the specifics of how many key North Pacific kelp species will perform and fare under projected SST and salinity remains unknown (Connell & Russell 2010, Fredersdorf et al. 2009, Krumhansl et al. 2014, Wernberg et al. 2010).

Insightful interpretations of possible threats to kelp communities rely on a firm understanding of the kelp life cycle, which can be described as an alternation of generations. To explain this alternation of generations further, adult kelps, or sporophytes, release sori (i.e., reproductive patches) that contain sporangia (spore producing structures), typically during the summer. Once these sori fall to the seafloor, zoospores are released into the water column as a means of offspring dispersal. They then settle onto the benthos, where the spores typically germinate within 24 hours by extruding the cytoplasm of the spore through the germ tube into the first gametophytic cell (Fletcher & Callow 1992). At this point in development, the spores have become gametophytes. Germ tubes of kelp gametophytes grow at mean rates of 20.62 ± 0.70 µm under normal conditions during the first 24 h post-settlement (Han et al. 2011). Further development into male and female gametophytes follows. These gametophytes produce eggs and sperm that fuse to form zygotes, which then ultimately develop into mature sporophytes, capable of beginning the reproductive cycle anew. Due to this alternation of generations, one way to better understand the effects of multiple stressors on kelp forests is to couple long-term monitoring of the adult kelp community with experimental work on their early life-history stages.

Spores represent a critical life stage for algal species as both dispersal and settlement occurs through the spore stage (Reed 1990). Spores must surpass obstacles (e.g., changes in temperature and salinity, physical barriers, strong currents, and over-shading by mature species) during the critical settlement and recruitment periods. The successful settlement of spores directly contributes to long-term community variability, as their dispersal, settlement, and recruitment aid in determining the future distribution of mature individuals. For the purposes of this study, settlement success was defined in terms of spore settlement density (at 24 hours, post-spore-release), the proportion of gametophytes to inviable attached spores (at 24 hours, post-spore release), and gametophyte growth (germ tube length at 7 days, post-spore-release). If rising SST and decreasing salinity alters, or even hinders, the ability of spores to settle and recruit, the effects will likely be reflected in long-term community composition. By exploring how multiple life-history stages of several key species are impacted by dual stressors, this research enhances our understanding of how kelps will respond to projected changes in SST and salinity, which may have important repercussions for the diverse ecosystems that these kelps support.

Study Species

This study tested the effects of increasing temperature and decreasing salinity on common North Pacific kelp species, including two canopy-forming and three understory species. Long-term biomass trends of the three understory species (*Agarum clathratum*, *Laminaria yezoensis*, and *Saccharina latissima*) were used to assess environmental impacts on adult kelps. Impacts on early life-history stages were assessed for the most common understory species in this region, *S. latissima*, and the two canopy species *Nereocystis luetkeana* and *Eualaria fistulosa*.

Agarum clathratum and *L. yezoensis* are both perennial understory species. *Agarum clathratum* distribution ranges from the Arctic Ocean and Bering Sea, Alaska to northern Washington; it can also be found in Russia, Japan, and Korea (Lindeberg & Lindstrom 2010). *Laminaria yezoensis* distribution ranges from the Bering Sea and Aleutian Islands, Alaska to Johnstone Strait, British Columbia, and also includes Japan and Russia (Lindeberg & Lindstrom 2010). The understory kelp, *Saccharina latissima* is also considered to be perennial, though some populations exhibit blade degradation in the winter, leaving only the stipes until spring when the blades regrow (Lindeberg & Lindstrom 2010). *Saccharina latissima* distribution ranges from the Arctic Ocean to Santa Catalina Island, California, and it can also be found in Russia, Japan, and Korea (Lindeberg & Lindstrom 2010). Sori form as dark patches on the blades of all three of these understory species.

The two canopy-forming species, *N. luetkeana* and *E. fistulosa*, are the only canopy-forming species present at the study site's high latitude (59° N). The annual *N. luetkeana* is the most prevalent canopy kelp throughout most of central and south-central Alaska, with its range extending from the eastern Aleutians (Umnak Island) to San Luis Obispo, California (Lindeberg & Lindstrom 2010). Sori form on surface blades of *N. luetkeana* and, after reaching maturity, drop to the benthos where spores are released. *Eualaria fistulosa* is another common annual kelp in central Alaska and is the only canopy-forming kelp in much of the Aleutians. Its distribution ranges from Russia/Japan to southern Southeast Alaska (Lindeberg & Lindstrom 2010). Sori develop on the reproductive sporophylls of *E. fistulosa*, which can be found on the upper stipe (i.e., supportive stalk) near the seafloor.

This study also tested the effects of increasing temperature and decreasing salinity on the macroalgal community associated with the target kelp species. In Kachemak Bay, these species included the Chlorophytes, *Acrosiphonia spp.*, *Codium spp.*, and *Monostroma grevillei*. Rhodophytes were more common and diverse and included *Bossiella plumosa*, *Callophyllis spp.*, *Constatinea spp.*, *Corallina spp.*, *Delesseria decipiens*, *Euthora cristata*, *Mastocarpus papillatus*, *Neoptilota spp.*, *Odonthalia floccosa*, *Opuntiella californica*, *Palmaria spp.*, *Polysiphonia pacifica*, *Pterosiphonia bipinnata*, and *Porphyra spp.* Ocrophytes included in this analysis were *Desmarestia spp.* and two additional brown kelp, *Alaria marginata* and *Cymathaere triplicate*, which were less abundant than the target kelp.

Objectives & Hypotheses

O1 Determine the relationships between populations of understory kelps (*Agarum clathratum*, *Laminaria yezoensis*, and *Saccharina latissima*) and associated macroalgal communities with interannual variations in sea surface temperature and salinity.

H1 Understory kelp biomass of each species is negatively correlated with increasing sea surface temperature and positively correlated with decreasing salinity.

H2 Associated macroalgal community biomass is negatively correlated with increasing sea surface temperature and positively correlated with decreasing salinity.

O2 Determine the effects of temperature and salinity on kelp spore settlement success of common North Pacific kelp species: *Nereocystis luetkeana*, *Eualaria fistulosa*, and *Saccharina latissima*.

H3 Spore settlement success across study species is negatively correlated with increasing temperature and positively correlated with decreasing salinity.

H4 Spore settlement success in *E. fistulosa* is the most negatively impacted under increasing temperature and decreasing salinity, followed by the more widely distributed species: *N. luetkeana*, and *S. latissima*.

METHODS:

Study Site Description

Kachemak Bay, Alaska is an elongated embayment contiguous with the southeastern entrance to Cook Inlet. The bay is 63 km long and 39 km wide at its entrance. It experiences an 8.7 m tidal range and input from seven glaciers along its southern shore (Field & Walker 2003). Regional circulation is characterized by an inflow of generally cyclonic ocean currents from the Gulf of Alaska. These currents enter Kachemak Bay primarily along its southern shore. Fresh water runoff from the surrounding glaciers and watersheds dilute the salinity and increase the sediment load as water circulates within the bay, before exiting along the north shore (Field & Walker 2003). Between 2002 and 2014, sea surface temperature (SST) in Kachemak Bay had a mean summer high (based on the average temperature during the single warmest 24-hour period, June-August of each year) of 12.2°C and a total annual range of -1.9°C to 13.6°C (NOAA NERRS water quality data 2002-2014). Between 2002 and 2014, salinity in Kachemak Bay had a mean summer low (based on the average salinity during the single least saline 24-hour period, June-August of each year) of 27.9 and a total annual range of 23.6 to 34.0 (NOAA NERRS water quality data 2002-2014).

The Macroalgal Community and Environmental Drivers

To determine relationships between populations of understory kelps and associated macroalgal community with interannual variations in sea surface temperature and salinity, a retrospective analysis was conducted on existing macroalgal community and environmental data. Kelp forest macroalgal community data were collected in Kachemak Bay, Alaska using consistent protocols in May of 2003, 2004, 2006, 2008, 2010, 2012, and 2014. Surveys of understory macroalgal biomass were conducted by divers at four kelp forests (Port Graham (PG), Outside Beach (OB), Elephant Island (EI), and Cohen Island (CI)) on the south side of Kachemak Bay (Fig. 1) along transects at 5-, 10-, and 15-m depth contours. Inconsistencies concerning annual sampling are as follows: Port Graham was not surveyed in 2003, Elephant Island was not surveyed in 2004, and Outside Beach was never sampled along a 15-m depth contour. Other than these exceptions, surveys quantified understory macroalgal biomass from scrapes of five randomly placed 0.25 m^2 quadrats along each transect at each site during all surveyed years. Each scrape was individually

bagged underwater and transported to the lab in a seawater-filled cooler. Once in the lab, samples were sorted and identified to the lowest possible taxonomic level, after which they were weighed to 0.1 g precision.

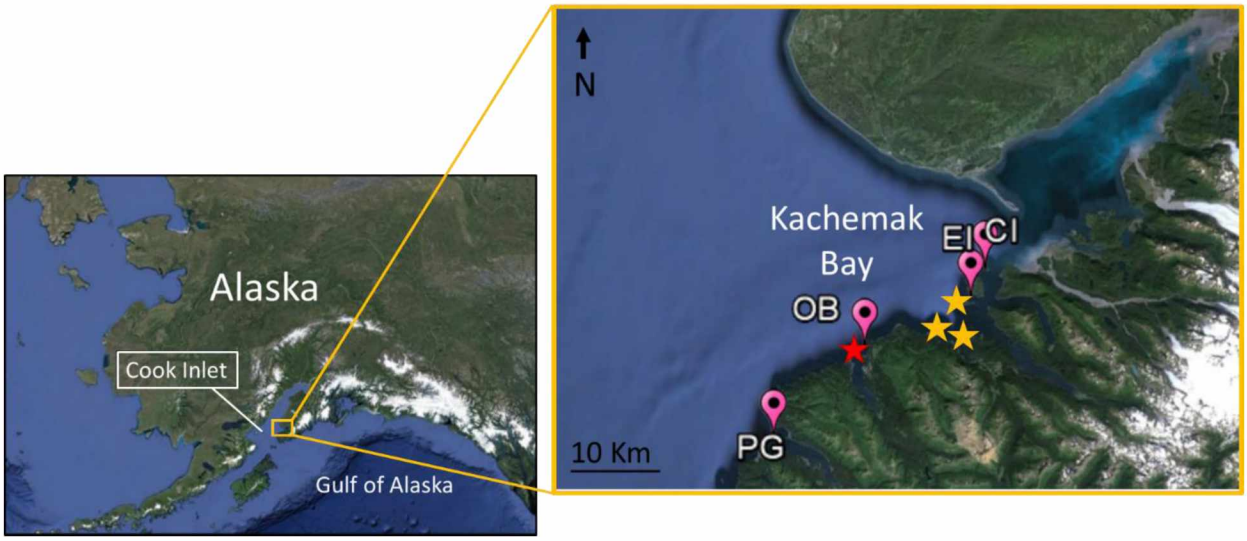

Fig. 1. Study Site Map
A map of Alaska (left) highlights the study site's location, denoted by the gold box in lower Cook Inlet. The map of Kachemak Bay (right) is a higher resolution image of the boxed study site. The surveyed kelp forests are marked and labeled (from left to right: Port Graham (PG), Outside Beach (OB), Elephant Island (EI), and Cohen Island (CI)). The temperature and salinity data logger's location is denoted by the red star (Seldovia ferry dock). The gold stars indicate sori collection sites for the spore experiment.

Complementary temperature and salinity data were collected, from 2003-2013, by a YSI electronic data logger located at the Seldovia ferry dock (Fig. 1). SST and salinity were recorded every 15 minutes from 1 m above the seafloor, with depths ranging from ~5-12.5 m, due to tidal cycles. The degree of precision for these temperature and salinity measurements was 0.01°C and 0.01, respectively. The top 5% of SST values for each year were averaged to derive annual SST maxima. Similarly, the bottom 5% of salinity values for each year were averaged to derive annual salinity minima.

Statistical Analyses – Macroalgae and the Environment

Understory kelp and associated macroalgal biomasses were totaled for individual taxa, annually, for each depth (5 m, 10 m, and 15 m), combining all sites. Species biomass totals were standardized by how many sites were surveyed during a given year and/or at a given depth to account for any sampling discrepancies. Environmental values analyzed include annual SST

maxima and salinity minima, or mean top 5% SST and mean bottom 5% salinity, respectively. A lag effect was applied, in which biological data were compared to environmental values from the year prior. This lag effect helps incorporate into the analyses conditions of the previous year that were experienced both by over-wintering perennial adults, developing sporophytes, and other fragile, early life history stages of macroalgae (i.e., spores and gametophytes).

To test hypothesis one, that the biomass of individual understory kelp species is negatively correlated with increasing sea surface temperature and positively correlated with decreasing salinity, Pearson's correlations were used. Environmental factors (SST maxima and salinity minima) were also tested against one another to determine if they were correlated. Pearson's r values greater than $|0.716|$ were considered significant, based on a 0.01 level of significance for a two-tailed test (df = 8). Canopy kelps were eliminated from these analyses because the quadrat design did not accurately measure these more patchily distributed species.

For hypothesis two, that associated macroalgal community biomass is negatively correlated with increasing sea surface temperature and positively correlated with decreasing salinity, multivariate analyses were used. These analyses examined variations in annual associated macroalgal community structure against SST and salinity trends using the software package PRIMER 7 & PERMANOVA+. Biological data were square root transformed to down-weight high biomass values. Macroalgal biomass resemblance matrices were calculated based on Bray-Curtis similarities. The BIOENV function (Spearman Rank Correlation method) and DistLM (distance based linear models) were used to evaluate relationships between environmental data (SST maxima and salinity minima) and patterns in macroalgal community annual biomass at each depth (5 m, 10 m, 15 m) from 2003-2014. Environmental factors remained offset by one year, as described above. P-values less than 0.05 were considered significant. Additionally, to determine which associated macroalgal species offered the greatest biomass contributions to the ecosystem, SIMPER (similarity percentage) analyses were conducted.

Factorial Spore Experiment

To determine the effects of SST and salinity on kelp spore settlement success and compare physiological thresholds between species, a laboratory experiment was conducted during the summer of 2015. For this experiment, sori (i.e., kelp reproductive structures) were collected

during biweekly boat and SCUBA searches for fertile individuals of *N. luetkeana*, *E. fistulosa,* and *S. latissima*. These sori are readily identified as dark patches on the blades of kelp (found at the surface in *N. luetkeana,* and near the benthos in *E. fistulosa* and *S. latissima*). Blades with ripe sori were removed from target kelp individuals and placed in a seawater-filled container for transport back to the laboratory. Since sori of these species do not all ripen concurrently (e.g., *N. luetkeana* typically ripens earlier in the summer than *E. fistulosa*), experimental trials were conducted throughout the summer (June-August).

In the laboratory, collected sori were lightly scrubbed and rinsed with 0.9-µm filtered seawater to remove impurities, such as macroscopic epiphytes or excess mucilage. Spores were then released in synchrony before each trial, following the methods described by Deiman et al. (2012). For this, the sori were packed in a cooler between layers of damp paper towels and plastic wrap and kept in the dark at 9°C for 30-60 minutes. Sori were then removed from the cooler and rinsed with 0.9-µm filtered seawater to remove any prematurely released spores, before being placed in individual beakers filled with 1.0 L of filtered seawater. Sori then remained at 9°C in these beakers under fluorescent light (250 lux) for 30-60 minutes. The solutions in the beakers became clouded with released spores and mucilage during this period. After using a cheesecloth to remove excess mucilage, the concentrations of resulting spore solutions were quantified using a hemocytometer (with a minimum detectable concentration of 2,000 spores/ml). All spore solutions were ultimately diluted to final concentrations of 4000 spores/ml in 400-ml volumes (1.6 million spores total, per trial) and placed in individual open-top plastic containers before experimental trials began.

One-half of the experimental solutions were diluted using 0.9-µm filtered seawater and remained at a seasonally ambient salinity of 31. Remaining spore solutions were diluted with a mixture of 0.9-µm filtered seawater and 0.9-µm filtered freshwater, resulting in a salinity of 26. Salinity was monitored and maintained throughout all experimental trials using a hand-held refractometer (±1 accuracy). Following dilutions, three clear glass microscope slides were placed at the bottom of each spore solution container to provide settlement substrate, after which spore solutions (with glass slides) were placed in temperature-controlled water baths under fluorescent light (250 lux). Individual containers were allowed to gradually rise to a given treatment temperature (13, 17, and 21°C) over the next 1-2 hours (or remain the same in the case of the 9°C/ambient controls).

Spore solutions remained exposed to temperature and salinity treatment conditions (Fig. 2) as spores were allowed to settle onto the glass slides for 24 hours, consisting of an 18-hour period of light exposure (the average summer day length in Kachemak Bay) and 6 hours of dark. The glass slides (three per trial) were then rinsed with 0.9-µm filtered seawater to remove any unattached spores. Settlement success was quantified under a compound microscope. Quantification was accomplished by haphazardly selecting five fields of view per slide at 400x magnification (0.17 mm^2) and counting the number of attached spores and/or gametophytes.

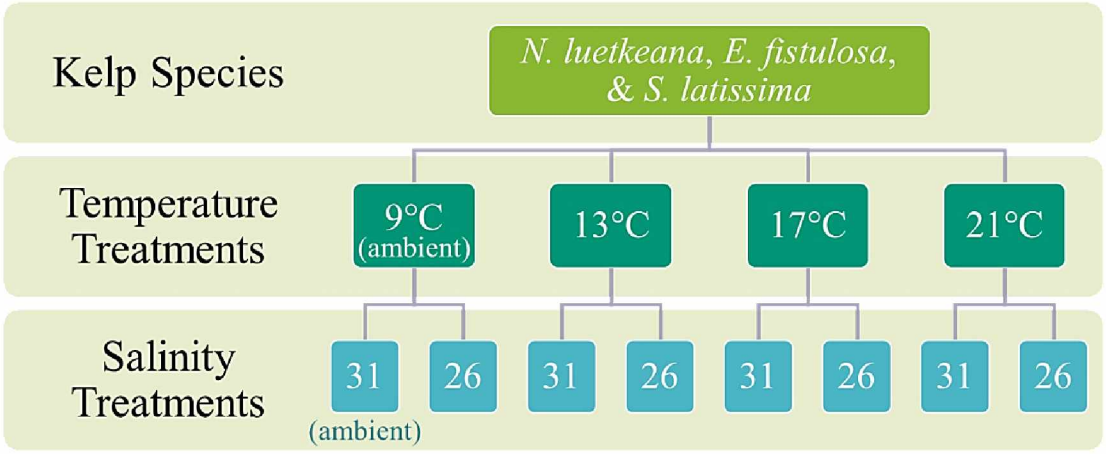

Fig. 2. Factorial Spore Experiment Design
A schematic of the factorial design spore experiment, illustrating the experimental treatment combinations that zoospores of the three study species were subjected to (n=5). Ambient summer seawater temperature and salinity of the study site are indicated.

Settlement slides were then returned to the same experimental conditions that they had previously been subjected to, this time in filtered seawater or seawater-freshwater solutions (no longer spore solutions). Gametophytes remained under experimental conditions for an additional six days, after which their short-term growth (at seven days post-spore-release) was quantified. Initial growth was measured from the outside of the original spore cell to the tip of the germ tube on each individual gametophyte. ImageJ software was used to process images of five haphazardly selected fields of view per slide at 400x magnification (0.17 mm^2). As an additional measure of performance, the proportion of gametophytes to nonviable attached spores (i.e., no germ tube present) was also recorded 24 hours after spore release. In total, five experimental settlement runs were conducted, per kelp species, under all eight combinations of temperature and salinity treatments (n=5).

Statistical Analyses – Spore Experiment

To determine the relative spore settlement success of each kelp species under the various temperature and salinity treatments, spore settlement concentrations and germ tube lengths were first averaged for each species under each of the eight treatments and standard errors were determined. Percentages of gametophytes versus inviable attached spores present at one week were also averaged between trials for species at each given treatment.

To test hypothesis three, that spore settlement success across study species was negatively correlated with increasing temperature and positively correlated with decreasing salinity, two separate two-way ANOVAs were performed. These ANOVAs compared spore settlement concentrations and germ tube growth, with experimental treatments and kelp species as the sources of variation in both cases. Three additional one-way ANOVAs were employed to test the effects of temperature and salinity on each of the three kelp species, separately. Response variables examined here were also spore settlement concentration and germ tube length.

Finally, to test which species' settlement success is the most negatively impacted under increased temperature and decreased salinity scenarios (hypothesis four), t-tests on observations of spore settlement concentrations and germ tube length were conducted. Three t-tests in total were performed, in reference to all possible species combinations (i.e., *E. fistulosa* versus *N. luetkeana*, *E. fistulosa* versus *S. latissima*, and *N. luetkeana* versus *S. latissima*). These comparisons were made for all eight experimental combinations of temperature and salinity conditions. P-values were considered significant at the $\alpha = 0.0167$ level, based on a post-hoc Bonferroni correction.

RESULTS:

Objective 1 – Relationships Between Adult Macroalgal Biomass and Environmental Factors

Annual SST maxima (mean top 5%) peaked in 2005 and exhibited a low in 2012, with a range of 9.95-12.32°C during the study period (2002-2014) (Fig. 3). Annual salinity minima (mean bottom 5%) peaked in 2013 and experienced a low in 2004, with a total range of 28.07-29.47 during the study period (Fig. 4).

Correlations between understory kelp biomass and SST maxima, across all three understory kelp species (*A. clathratum, L. yezoensis*, and *S. latissima)*, at all three depths (5 m, 10 m, and 15 m) were not statistically significant, with the exception of *L. yezoensis* at 10 m (Table 1). Negative correlations between *A. clathratum, L. yezoensis*, and *S. latissima* biomass at 5 m and annual SST maxima (Pearson's r = -0.4538, -0.2769, and -0.2336, respectively) were all weak. Negative correlations at 10 m were similarly weak in *A. clathratum* and *S. latissima* (Pearson's r = -0.2409 and -0.1372, respectively), but statistically significant for *L. yezoensis* (Pearson's r = -0.7227), as mentioned above (Table 1). Negative correlations between *A. clathratum, L. yezoensis*, and *S. latissima* biomass at 15 m and annual SST maxima (Pearson's r = -0.4590, -0.0640, and -0.0918, respectively) were all weak. No significant correlations between understory kelp species biomass and annual salinity minima were found. In addition, no correlation was found between annual SST maxima and annual salinity minima.

Additionally, SST maxima and salinity minima, both separately and together, were determined to be insignificant factors in shaping the associated macroalgal community biomass at all depths (Table 2). Species considered in this analysis of the macroalgal community include *Acrosiphonia spp.*, *Alaria marginata*, *Bossiella plumosa*, *Callophyllis spp.*, *Codium spp.*, *Constatinea spp.*, *Corallina spp.*, *Cymathaere triplicata*, *Delesseria decipiens*, *Desmarestia spp.*, *Euthora cristata*, *Mastocarpus papillatus*, *Monostroma grevillei*, *Neoptilota spp.*, *Odonthalia floccosa*, *Opuntiella californica*, *Palmaria spp.*, *Polysiphonia pacifica*, *Pterosiphonia bipinnata*, and *Porphyra spp.* SIMPER analyses indicated that dominant taxa composing the macroalgal community fluctuated through time, despite the lack of significant correlations with SST and salinity (Fig. 5). For instance, though the 15-m community during 2004-2008 and 2012 was dominated by *Polysiphonia/Pterosiphonia*, during 2003, 2010, and 2014 *O. floccosa*, *Palmaria spp.*, and *Desmarestis spp.*, respectively, offered the greatest percent contributions.

Objective 2 – Effects of temperature and salinity on kelp spore settlement success

Eualaria fistulosa spore settlement exhibited a significant decrease in concentrations, from ~15 spores per field of view under the ambient treatment (9°C/31 salinity) to ~5 spores and fewer

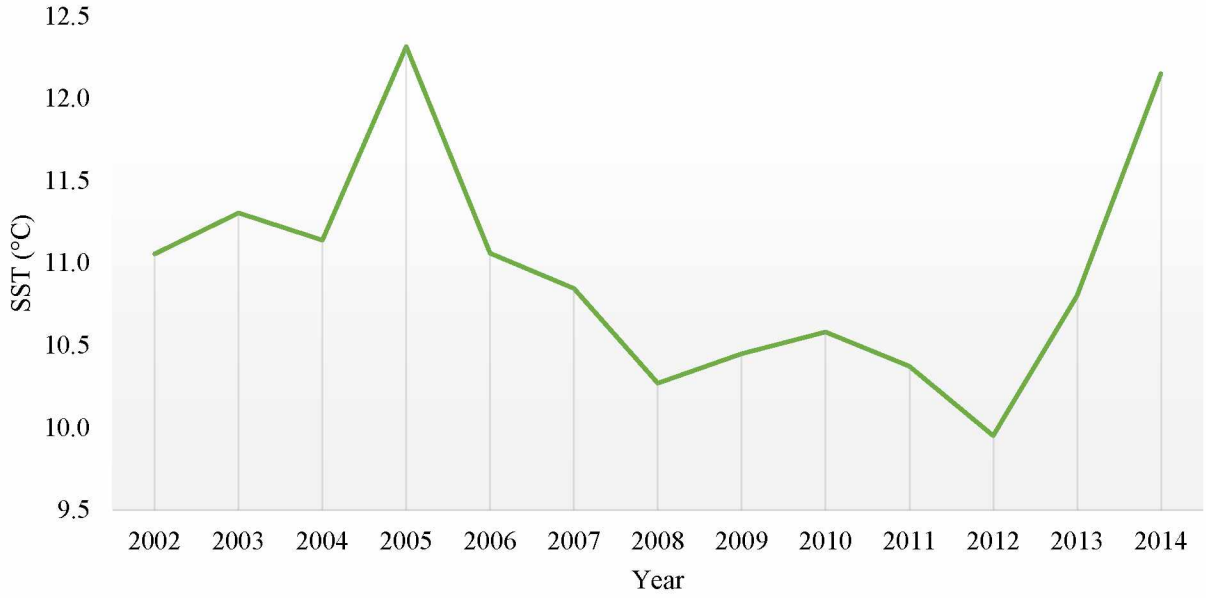

Fig. 3. SST Maxima
Annual SST maxima (mean top 5%) are shown from 2002-2014.

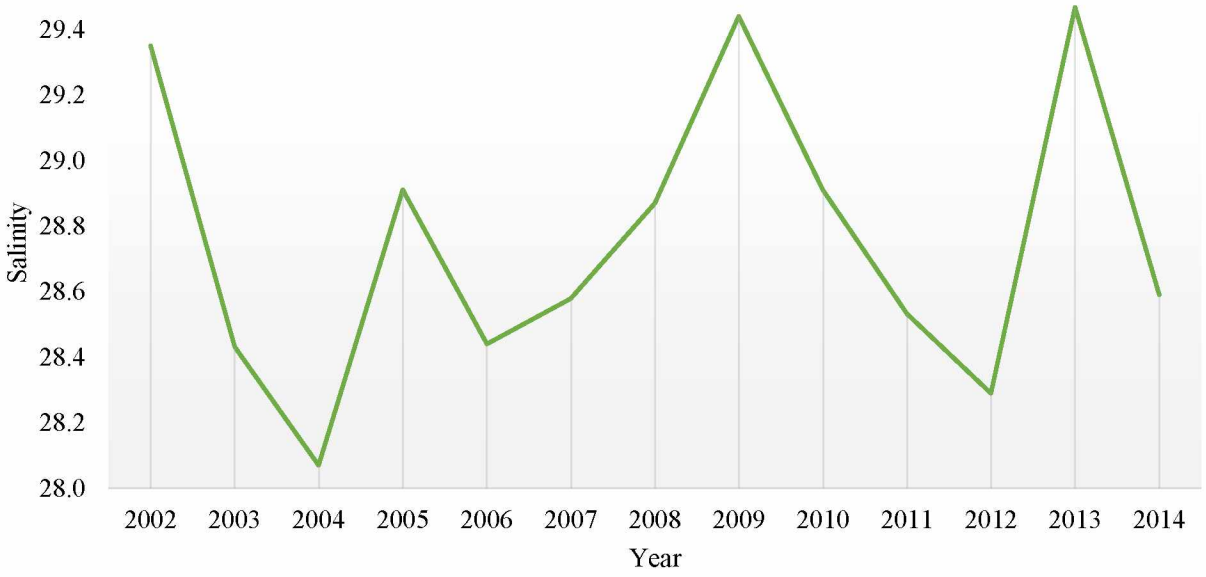

Fig. 4. Salinity Minima
Annual salinity minima (mean bottom 5%) are shown from 2002-2014.

Table 1. Pearson Correlations (Kelp and Environmental Factors)
Pearson's r values comparing the annual biomass densities of the understory kelps *Agarum clathratum* (AC), *Laminaria yezoensis* (LY), and *Saccharina latissima* (SL) at depths of a) 5 m, b) 10 m, and c) 15 m with annual SST maxima and annual salinity minima values from the previous year. The critical Pearson's r value for these tests was 0.716, based on a 0.01 level of significance for a two-tailed test (df = 8). Significant values (Pearson's r > $\left|0.716\right|$) are marked in bold.

a) 5 m

	AC	*LY*	*SL*	*SST*
SST	-0.4538	-0.2769	-0.2336	1
Salinity	0.0533	-0.1764	-0.2817	-0.1344

b) 10 m

	AC	*LY*	*SL*	*SST*
SST	-0.2409	**-0.7227**	-0.1372	1
Salinity	-0.3160	0.2644	-0.4309	-0.1344

c) 15 m

	AC	*LY*	*SL*	*SST*
SST	-0.4590	-0.0640	-0.0918	1
Salinity	0.6072	-0.4741	-0.3526	-0.1344

Table 2. BIOENV Results (Macroalgal Community)
BIOENV correlations (Spearman Rank Correlation method) between environmental factors (SST maxima and salinity minima) and species biomass annual totals (2003-2014) for associated macroalgae at each depth (5 m, 10 m, and 15 m). DistLM (distance based linear models) p-values less than 0.05 were considered significant.

	5 m		10 m		15 m	
	Corr.	*p*	*Corr.*	*p*	*Corr.*	*p*
SST maxima	-0.037	0.503	-0.103	0.637	-0.020	0.152
Salinity minima	0.132	0.198	0.087	0.376	0.259	0.109
SST max, Salinity min	0.025		-0.031		0.129	

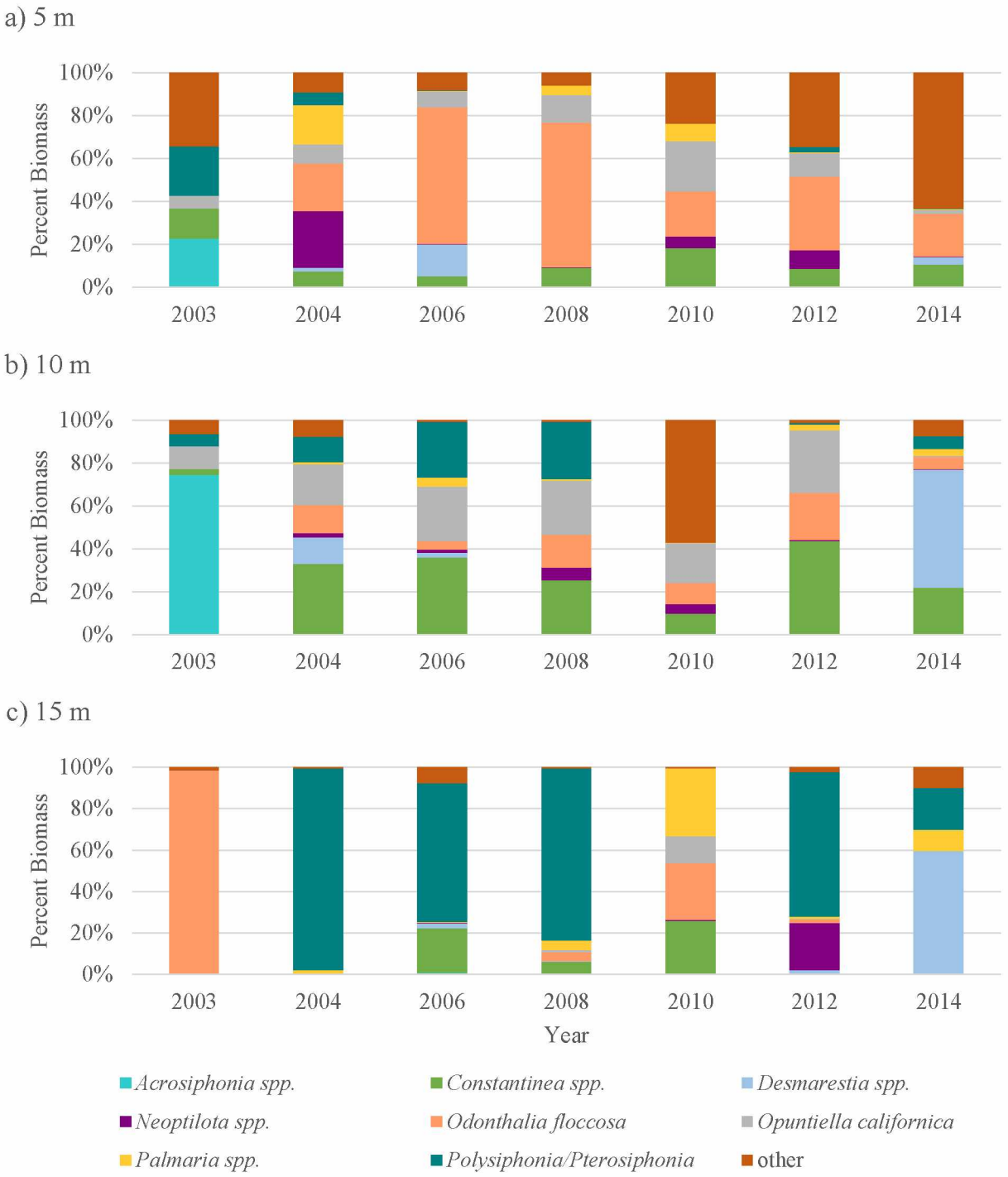

Fig. 5. Associated Macroalgal Community Composition

Annual percent contributions of species biomass to the associated macroalgal community at each depth: a) 5 m, b) 10 m, c) 15 m, from 2003-2014. Included species contributed more than 25% to similarities among sites during at least one year, based on SIMPER analyses. "Other" consists of *Alaria marginata*, *Bossiella plumosa*, *Callophyllis spp.*, *Codium spp.*, *Corallina spp.*, *Cymathaere triplicata*, *Delesseria decipiens*, *Euthora cristata*, *Mastocarpus papillatus*, *Monostroma grevillei*, and *Porphyra spp.*

under more extreme treatments (13°C and greater, both salinities) (Fig. 6a). More gradual, but still significant, declines in spore settlement under increased temperature and decreased salinity were observed in *N. luetkeana* and *S. latissima* (Fig. 6b & c). *Nereocystis luetkeana* spore settlement was highest under the ambient treatment (9°C/31 salinity) with ~24 spores per field of view, and never dropped below ~5 spores per field of view (Fig. 6b). *Saccharina latissima* spore settlement was also highest under the ambient treatment (9°C/31 salinity) with ~17 spores per field of view, and only fell below ~5 spores under the most extreme treatment (12°C/26 salinity) (Fig. 6c).

Average germ tube length at 7 days in *E. fistulosa* declined from 20.95 µm under the ambient treatment (9°C/31 salinity) to less than 5 µm under more extreme treatments (17 and 21°C, both salinities) (Fig. 7a). By contrast, *N. luetkeana* and *S. latissima* gametophytes exhibited germ tubes longer than 5 µm under all treatment conditions except the most extreme (12°C/26 salinity), at which average germ tube length was 4.95 µm and 2.66 µm, respectively (Fig. 7b & c). Settlement concentration and germ tube length significantly declined across all three species as temperature increased and salinity decreased (from the ambient treatment of 9°C/31 salinity, to the extreme treatments of 17 and 21°C, both salinities) (Fig. 5 & 6, Table 4). However, *N. luetkeana* gametophyte growth peaked at ~23 µm under the 13°C treatments, before declining significantly (Fig. 7b).

Experimental treatment and kelp species both played statistically significant roles in shaping spore settlement success, defined as spore settlement concentration (p-value < 0.0001 for both factors) and gametophyte growth/germ tube length (p-value < 0.0001 and p-value = 0.0200 for treatment and species, respectively) (Table 3). The interactions of experimental treatments and kelp species were an insignificant factor in terms of shaping spore settlement concentrations and germ tube length, with p-values of 0.2826 and 0.2534, respectively (Table 3). The effect of variations in temperature was significant for spore settlement concentration amongst all three study species (p-value < 0.0001 for both *E. fistulosa* and *S. latissima*, and p-value = 0.0003 for *N. luetkeana*) (Table 4). The effect of variations in temperature was also found to be significant for germ tube growth in all three study species (p-value < 0.0001 for all three species) (Table 4). Additionally, variation in salinity had a significant effect on spore settlement concentration in *S. latissima* (p-value < 0.0001) and on germ tube length across all three species (p-value = 0.0029,

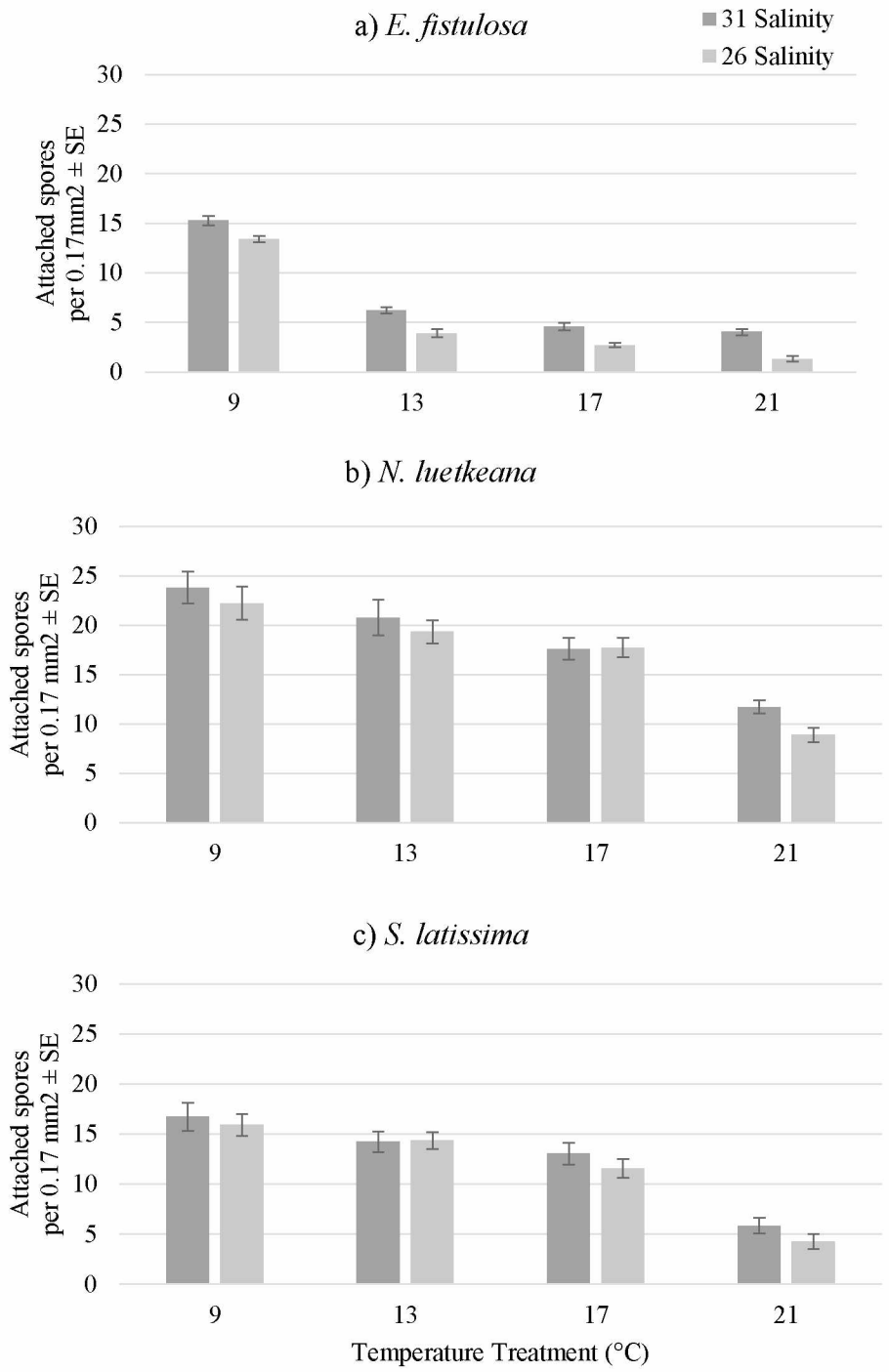

Fig. 6. Spore Settlement
Effects of temperature (9, 13, 17, and 21°C) and salinity (26 and 31) treatments on spore settlement concentration are shown for *E. fistulosa*, *N. Luetkeana*, and *S. latissima* at 24 hours post-spore-release. Concentrations represent the mean quantity of attached spores per field of view at 400x (field of view area = 0.17 mm^2) for each species under each combination of experimental conditions (n = 5).

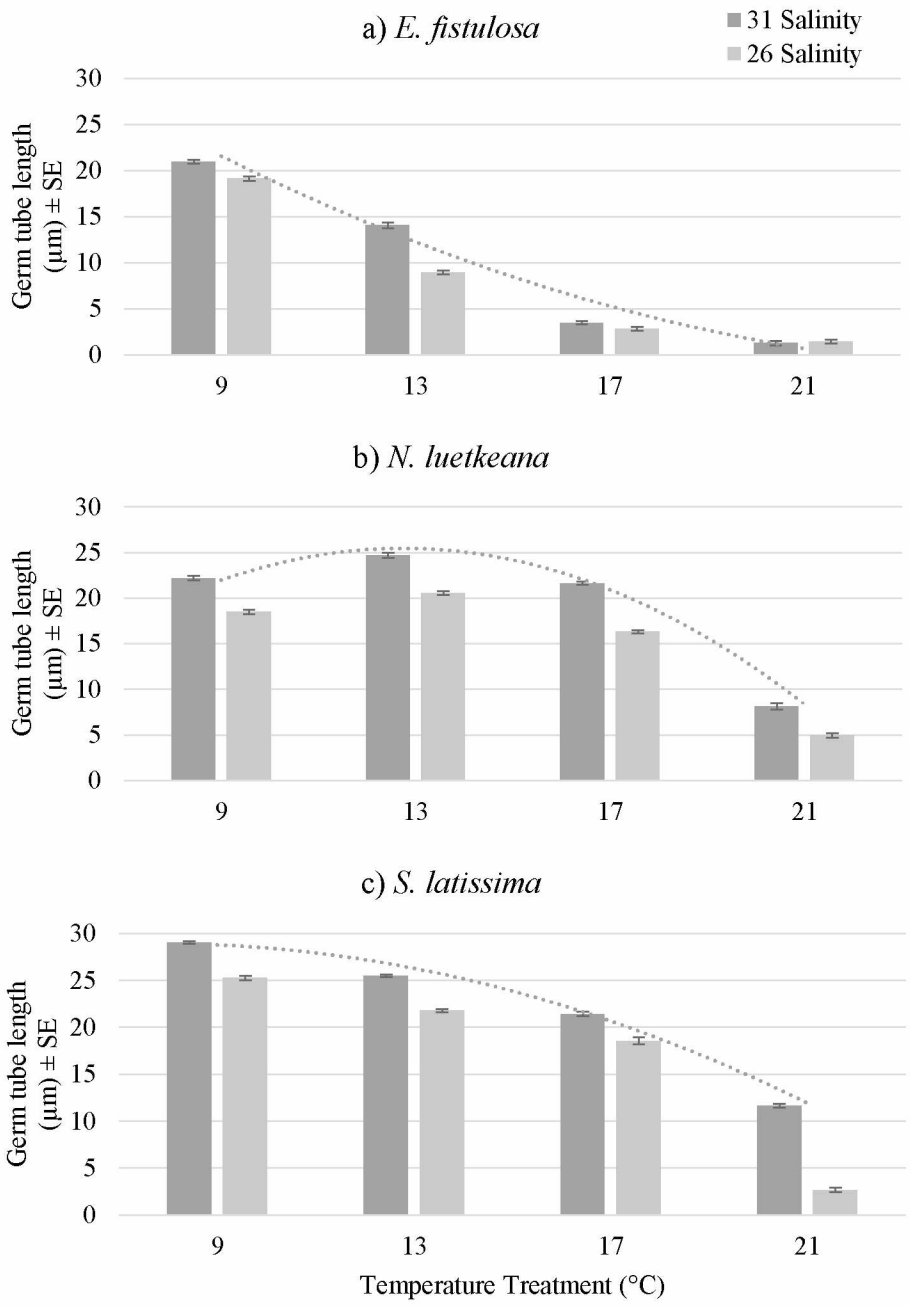

Fig. 7. Gametophyte Growth
Effects of temperature (9, 13, 17, and 21°C) and salinity (26 and 31) treatments on germ tube length are shown for *E. fistulosa*, *N. Luetkeana*, and *S. latissima* at 7 days, post-spore-release. Values represent the mean germ tube length measured for each species under each combination of experimental conditions (n = 5). Dotted lines represent 2nd degree polynomial regressions, illustrating the non-linear relationships between temperature and germ tube length for the 31 salinity treatment. Regressions for the 26 salinity treatment showed similar trends, but are not shown here for ease of view.

Table 3. ANOVA Results (Significance of Treatment and Species)
Two-way analyses of variance (ANOVA) results comparing a) spore settlement concentrations and b) germ tube length between experimental treatments (8 temperature-salinity combinations) and between kelp species (*E. fistulosa*, *N. luetkeana*, and *S. latissima*). Values significant at the $\alpha = 0.05$ level are marked in bold.

a)

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Experimental Treatment	2248.832	7	321.262	17.391	**<0.0001**	2.106
Kelp Species	2560.838	2	1280.419	69.314	**<0.0001**	3.091
Interaction	312.346	14	22.310	1.208	0.2826	1.796
Within	1773.392	96	18.473			
Total	6895.408	119				

b)

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Experimental Treatment	4125.579	7	589.368	30.036	**<0.0001**	2.156
Kelp Species	111.716	1	111.716	5.693	**0.0200**	3.991
Interaction	181.937	7	25.991	1.325	0.2534	2.156
Within	1255.794	64	19.622			
Total	5675.025	79				

Table 4. ANOVA Results (Effects on Species)
Results of ANOVAs on effects of: temperature (9, 13, 17, and 21°C) and salinity (26 and 31) on a) *E. fistulosa* (EF) b) *N. luetkeana* (NL) and c) *S. latissima* (SL). The response variables are spore settlement concentration (SSC) and germ tube length (GTL). Values significant at the $\alpha = 0.05$ level are marked in bold.

a) EF

		SSC		GTL	
Source of Variation	*df*	*F*	*P-value*	*F*	*P-value*
Temperature	3	359.309	**<0.0001**	221.385	**<0.0001**
Salinity	1	59.989	**<0.0001**	10.437	**0.0029**

b) NL

		SSC		GTL	
Source of Variation	*df*	*F*	*P-value*	*F*	*P-value*
Temperature	3	8.439	**0.0003**	17.258	**<0.0001**
Salinity	1	0.594	0.4464	5.522	**0.0251**

c) SL

		SSC		GTL	
Source of Variation	*df*	*F*	*P-value*	*F*	*P-value*
Temperature	3	12.196	**<0.0001**	83.656	**<0.0001**
Salinity	1	0.438	0.5127	25.797	**<0.0001**

0.0251, and p-value < 0.0001 for *E. fistulosa*, *N. luetkeana*, and *S. latissima*, respectively) (Table 4).

As a further assessment of settlement success, proportions of gametophytes to attached inviable spores were significantly greater in *N. luetkeana* and *S. latissima* compared to *E. fistulosa*, under the 13°C/26 salinity treatment and both 17°C treatments (Fig. 8). However, under the most extreme treatments (21°C/26 salinity and 21°C/31 salinity), there were no significant differences between *N. luetkeana* and *E. fistulosa*. *Eualaria fistulosa* was the only species to produce no gametophytes under experimental conditions (21°C/31 salinity).

Nereocystis luetkeana displayed significantly higher spore settlement densities compared to *E. fistulosa* under both salinity conditions at increased temperatures of 13°C, 17°C, and 21°C (Fig. 5a & b, Table 5a). *N. luetkeana* similarly displayed significantly greater germ tube lengths compared to *E. fistulosa* under 13°C/26 salinity, and 17°C and 21°C at both salinities (Fig. 6a & b, Table 5a). Likewise, *S. latissima* displayed significantly higher spore settlement densities compared to *E. fistulosa* under both salinity treatments at 13°C and 17°C (Fig. 5a & c, Table 5b). Both species performed poorly under 21°C treatments. *Saccharina latissima* also exhibited significantly greater germ tube lengths under all experimental conditions, except the most extreme treatment of 21°C/26 salinity (Fig. 7a & c, Table 5b). Both species performed equally poorly under 21°C/26 salinity.

When compared to each other, *N. luetkeana* and *S. latissima* displayed no significant differences in spore settlement and gametophyte growth under nearly all treatments. However, *N. luetkeana* spore settlement concentration was significantly higher under 21°C/31 salinity (Fig. 6b & c, Table 5c). *Saccharina latissima* germ tube length, on the other hand was significantly greater than *N. luetkeana* germ tube length under conditions of 9°C/26 salinity (Fig. 7b & c, Table 5c).

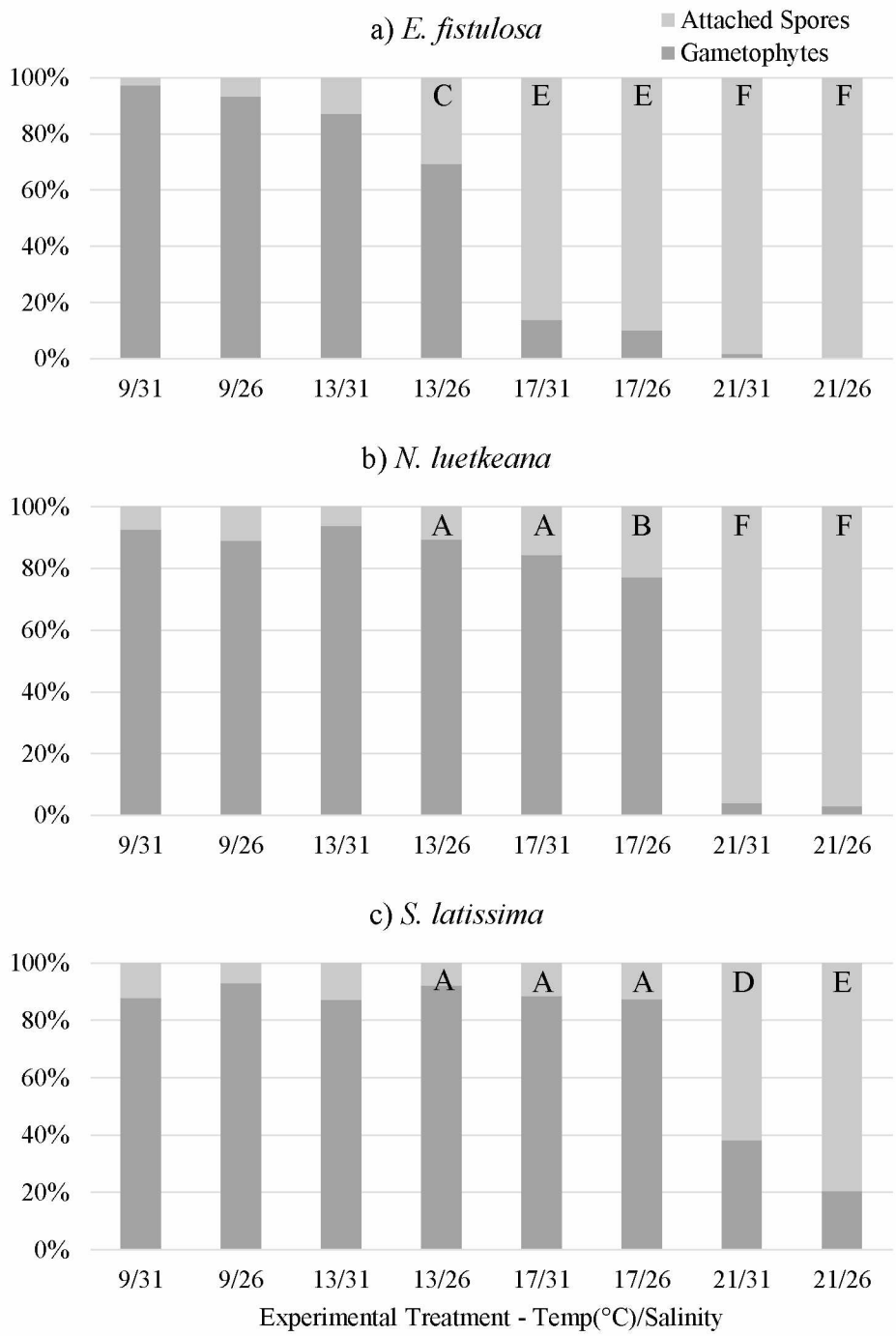

Fig. 8. Proportion of Gametophytes to Inviable Attached Spores
Effects of temperature (9, 13, 17, and 21°C) and salinity (26 and 31) treatments on proportions of gametophytes, versus nonviable attached spores, are shown for *E. fistulosa*, *N. Luetkeana*, and *S. latissima* at 24 hours, post-spore-release. Values represent the average percent of gametophytes vs. spores for each species under each combination of experimental conditions (n = 5). Letters indicate intra- and interspecific significant differences, with progression in alphabetical order corresponding to decreased performance (i.e., greater percent of inviable individuals).

Table 5. T-test Results (Interspecific Comparisons)
Results of t-test on paired observations of spore settlement concentrations and germ tube length of a) *E. fistulosa* versus *N. luetkeana* b) *E. fistulosa* versus *S. latissima* and c) *N. luetkeana* versus *S. latissima*. The comparison is made for experimental combinations of temperature (9, 13, 17, and 21°C) and salinity (26 and 31) (df = 8). Values significant at the $\alpha = 0.0167$ level, based on the Bonferroni correction, are marked in bold.

a)

Experimental Treatment		Spore Settlement (EF vs. NL)		Germ Tube Length (EF vs. NL)	
Temperature	Salinity	t-value	p-value	t-value	p-value
9°C	31	-2.308	0.04987	-0.486	0.63984
	26	-2.408	0.04267	0.326	0.75301
13°C	31	-3.822	**0.00507**	-2.610	0.03113
	26	-6.335	**0.00022**	-3.928	**0.00437**
17°C	31	-5.638	**0.00049**	-5.563	**0.00053**
	26	-9.967	**0.00001**	-5.679	**0.00047**
21°C	31	-7.244	**0.00009**	-7.197	**0.00009**
	26	-7.634	**0.00006**	-4.123	**0.00333**

b)

Experimental Treatment		Spore Settlement (EF vs. SL)		Germ Tube Length (EF vs. SL)	
Temperature	Salinity	t-value	p-value	t-value	p-value
9°C	31	-0.536	0.60642	-3.993	**0.00399**
	26	-1.031	0.33255	-3.479	**0.00834**
13°C	31	-4.023	**0.00382**	-8.692	**0.00002**
	26	-7.582	**0.00006**	-10.424	**0.00001**
17°C	31	-3.402	**0.00933**	-9.261	**0.00002**
	26	-5.321	**0.00071**	-11.946	**<0.00001**
21°C	31	-1.163	0.27832	-5.876	**0.00037**
	26	-1.882	0.09656	-1.290	0.23295

c)

Experimental Treatment		Spore Settlement (NL vs. SL)		Germ Tube Length (NL vs. SL)	
Temperature	Salinity	t-value	p-value	t-value	p-value
9°C	31	1.590	0.15052	-2.818	0.02255
	26	1.446	0.18632	-3.280	**0.01118**
13°C	31	1.521	0.16667	-0.190	0.85407
	26	1.847	0.10187	-0.405	0.69586
17°C	31	1.351	0.21361	0.053	0.95885
	26	2.756	0.02483	-0.830	0.43071
21°C	31	3.195	**0.01272**	-1.774	0.11402
	26	2.518	0.03591	2.035	0.07628

DISCUSSION:

This study suggests that under projected increases in temperature and decreases in salinity, the responses of North Pacific kelp species are both life-stage-specific and species-specific. Based on these findings, early life-history stages (e.g., spores and gametophytes) and species with narrower ranges (distribution restricted to higher latitudes) appear to be especially vulnerable to impending climatic changes.

Adult understory kelp populations of *A. clathratum*, *L. yezoensis*, and *S. latissima* and associated macroalgal communities were largely unaffected by interannual fluctuations in SST and salinity. It is important to note that, although the findings detailed here are based on one particular definition of SST maxima and salinity minima (average annual top 5% and bottom 5%, respectively), analyses did not appear to be sensitive to these choices. Further analyses (not shown here) were conducted in which additional environmental metrics (average annual top and bottom 10, 15, and 30%; annual means; and annual ranges) were considered and resulted in a similar lack of significant correlations between the environment and biota.

The overall lack of response displayed by these adult kelps and associated macroalgal populations under annual changes in SST and salinity could be due to several factors. First, the study was restricted to *in situ* observations during a relatively small (12-year) period. The range of salinity and temperature extremes experienced during this window of time may have been too narrow to dramatically impact the system and manifest in biomass changes of understory kelp populations or associated macroalgal communities. However, such changes may have already occurred prior to monitoring efforts. For instance, a longer study concerning a related kelp species (*Macrocystis pyrifera*) revealed dramatic changes in kelp biomass over a century, and attributed them to a variety of factors including temperature change (Tegner et al. 1996). Second, tracking annual species biomass in a natural setting reflects the ability of these populations to gradually adapt to environmental change. Significant quantitative differences in physiological responses to environmental stressors have been observed in geographically isolated populations of kelp, and it has been suggested that climatic change may select for ecotypes that are best suited to changing environmental regimes (Kopczak et al. 1991). Third, other site-specific factors such as sedimentation, light limitation, wave exposure, and biotic interactions (e.g.,

herbivory) may play a larger role in shaping these populations, masking any possible additional effects of salinity and temperature on biomass. For example, light limitation due to chronic fog cover has been suggested as a key factor in determining the abundance and distribution of *Nereocystis* in the Aleutians, as opposed to thermal constraints alone (Miller & Estes 1989). Another study implicated herbivory as a factor that can overshadow the role of an abiotic driver, in this case wave action, in determining the distribution and abundance of kelps (Duggins et al. 2001).

The general absence of significant correlations between adult kelp species biomass and variations in SST and salinity, however, does not confirm a lack of response to these stressors in these species overall, as vulnerability to environmental obstacles/stressors is often life-stage specific (Fredersdorf et al. 2009). Dispersal and settlement of kelps occur through the critical early life-history stages (e.g., spores and gametophytes) (Reed 1990). Accordingly, successful recruitment is key in shaping the distribution and abundance of adult populations. Any effects, positive or negative, of temperature and salinity regimes on early life-history stages will directly impact resulting adult populations, ultimately shaping long-term community assemblages. In a controlled laboratory setting, the early life-history stages of *E. fistulosa*, *N. luetkeana*, and *S. latissima* experienced significant negative impacts under projected changes in temperature and salinity conditions. Both spore settlement concentration, proportion of gametophytes to inviable attached spores, and germ tube growth decrease across *E. fistulosa*, *N. luetkeana*, and *S. latissima* under increasing temperature and decreasing salinity. The degree of decline in settlement success is species-specific, with *N. luetkeana* and *S. latissima* generally outperforming *E. fistulosa*. Other studies have shown similarly negative impacts of climate change related stressors on kelp early life-history stages. For instance, increased levels of pCO_2 and temperature have been linked to increased kelp spore mortality and decreased germination rates in a related species, *Macrocystis pyrifera* (Gaitán-Espitia et al. 2014). Other species of macroalgae, however, experienced strong negative impacts of sedimentation on recruitment success but no temperature-induced effects on recruitment, survival, or growth (Irving et al. 2009). Such varied findings highlight the necessity to explore the species-specific nature of interactions between macroalgae and environmental stressors.

Outperformance of *E. fistulosa* by *N. luetkeana* and *S. latissima* in terms of spore settlement concentration, proportion of gametophytes to inviable attached spores, and gametophyte growth, under increased temperatures and decreased salinities could be attributable to *E. fistulosa's* relatively narrow range. The population of *E. fistulosa* examined in this study was near the southern extent of its range (southern Southeast Alaska), as opposed to the more widely distributed *N. luetkeana* and *S. latissima* (found as far south as Central and Southern California, respectively). This imbalance in distribution could be a result of inherent differences in the ability of these species to cope with changes in latitudinal gradients of temperature and salinity. Differences in the latitudinal ranges of adult macroalgae have been linked to variations in thermal tolerance, as species with lower latitude distributions were found to be more heat-tolerant while species with a higher latitude terminus to their range were more cold-tolerant (Smith & Berry 1986). The relatively far-reaching southern range of *N. luetkeana* could also help to explain why gametophyte growth peaked under the moderately warmed treatment of 13°C, as this would be a more typical environmental condition at its lower, mid-range latitudes. Although, why gametophyte growth in *S. latissima* and spore settlement in both species would not also follow this trend remains unclear.

Since kelps are foundation species, they provide complex structure necessary to support diverse associated communities of a wide array of both ecologically and commercially important taxa (Dayton 1985, Bologna & Steneck 1993, Seitz et al. 2014, Thornton & Herbert 2014). Environmental impacts on key taxa, such as foundation species, are known to result in cascading effects on the community at large due to ecological interactions (Schiel et al. 2004). Therefore, impacts to kelp populations are likely to have indirect effects, altering kelp forest ecosystems as a whole. For instance, future change that results in declines of canopy kelps could have a positive indirect impact on understory species due to competitive release, since canopy species are known to typically inhibit the growth of understory species through domination of light and space (Irving & Connell 2006, Russell 2007). Additionally, differences in fish communities can be linked to presence and type of marine vegetation available in a given habitat (Hamilton & Konar 2007). Different kelp species assemblages provide varied levels of protection from predators and attract different prey, which in turn affects the diversity of fishes supported by the ecosystem (Dean et al. 2000). Sites with the presence of both canopy and understory kelp species are capable of supporting higher densities of fish, compared to sites with understory species alone

(Hamilton & Konar 2007). Hence, insights into how ecosystem engineers, like kelps, will be impacted by projected environmental change are invaluable in assessing how the distribution and abundance of associated species are likely to transform through time. This improved understanding of which species will be most impacted under multiple climate change induced stressors can aid in the design of effective management strategies by targeting the preservation of more vulnerable species and the foundation species they rely on to persist.

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